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THALASSOCALYCE INCONSTANS, NEW GENUS AND SPECIES, AN ENIGMATIC CTENOPHORE REPRESENTING A NEW FAMILY AND ORDER

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ABSTRACT

Thalassocalyce inconstans, new genus and species, is an unusual, medusa-shaped ctenophore collected in slope water off the coast of New England. It is morphologically distinct from both cydippid and lobate ctenophores, and forms the basis of a new order of the Ctenophora, Thalassocalycida and consequently a new family. Similarities to previously described medusoid larvae of ctenophores suggest a recapitulation of the thalassocalycid morphology in the ontogeny of other species.

The members of the phylum Ctenophora share a rather simple basic body plan, but have evolved into a wide variety of forms, including both pelagic and benthic species. Over two hundred species of pelagic ctenophores have been described in the last two centuries. Many of these have since been synonymized; others appear to be valid species but have rarely been reported since the time of their original descriptions. The extreme fragility of ctenophores makes them difficult to collect intact and almost impossible to preserve, and is responsible for much of the taxonomic confusion in oceanic species. In contrast, certain abundant and hardy neritic species, such as *Pleurobrachia pileus* (Fabricius, 1780), *Mnemiopsis leidyi* Agassiz, 1865, and *Beroe cucumis* Fabricius, 1780, are readily collected close to marine biological stations, and have quite naturally become the "typical" ctenophores (Barnes, 1974).

Many ctenophores that are considered to be rare are rare only in plankton samples. Often, species which actually are abundant in the ocean are too delicate to survive conventional plankton collecting methods. We have demonstrated elsewhere (Harbison, Madin, and Swanberg, 1978) that this is true of several oceanic forms. The species we describe in this paper is one of the most delicate we have seen, so it is not surprising that it has not been reported previously. The morphology of *Thalassocalyce inconstans*, new genus and species, is so different from that of any other ctenophore that we are compelled to erect a new order, Thalassocalycida, for it, following the precedent of Moser (1907) with the Ganeshida. Three presumed larval stages of other ctenophores have been described, which resemble the species we describe here. We will discuss the affinities of these larvae with *T. inconstans*.

METHODS

Specimens of *Thalassocalyce inconstans* were found by SCUBA divers in the top 30 m. The dive stations were made in Slope Water and the northern Sargasso Sea; Table 1 lists dates, positions and surface temperatures for these stations. *Thalassocalyce inconstans* was observed or collected on only 19 out of 250 dives made from 1975 through 1977. The feeding biology and distribution of this species is discussed by Harbison, Madin, and Swanberg (1978).

Observations, photographs and drawings were made of live animals maintained in shipboard aquaria. Specimens could be kept for 5–7 days without feeding, although they became smaller. A total of 16 individuals were collected on nine of the dives listed in Table 1; 10 of these were examined in detail and form the basis of this paper. We were able to preserve only one specimen in 5% buffered Formalin, and the morphologi-

Table 1. Stations where *Thalassocalyce inconstans* was collected or observed

Station Number	Position	Date	Surface Temperature (C)
267	32°18′N, 63°00′W	21 September 1973	—
405	34°11′N, 71°38′W	11 August 1975	27.4
511	38°22′N, 66°20′W	30 July 1976	24.7
512	38°35′N, 66°28′W	31 July 1976	25.0
514	39°08′N, 72°38′W	20 August 1976	24.0
515	39°05′N, 72°28′W	20 August 1976	24.0
516	38°28′N, 72°01′W	21 August 1976	23.6
518	38°57′N, 72°24′W	22 August 1976	23.0
519	39°07′N, 72°14′W	23 August 1976	—
520	38°50′N, 72°27′W	23 August 1976	—
521	38°55′N, 72°59′W	24 August 1976	23.4
523	39°15′N, 72°00′W	25 August 1976	—
525	38°58′N, 72°23′W	28 August 1976	23.7
527	38°57′N, 72°25′W	30 August 1976	22.8
528	38°47′N, 71°47′W	31 August 1976	21.6
529	38°44′N, 71°46′W	31 August 1976	22.3
530	38°26′N, 72°07′W	1 September 1976	22.8
533	38°52′N, 72°19′W	4 September 1976	—
583	36°44′N, 63°26′W	24 July 1977	26.0

cal description given here is based on direct observations and photographs of living animals.

THALASSOCALYCIDA new order

The characters of the order are combined with those of the sole species described below.

THALASSOCALYCIDAE new family

The characters of the family are combined with those of the sole species described below.

Thalassocalyce new genus

The characters of the genus are combined with those of the sole species described below.

Type-species—***Thalassocalyce inconstans*** new species

Figures 1 and 2

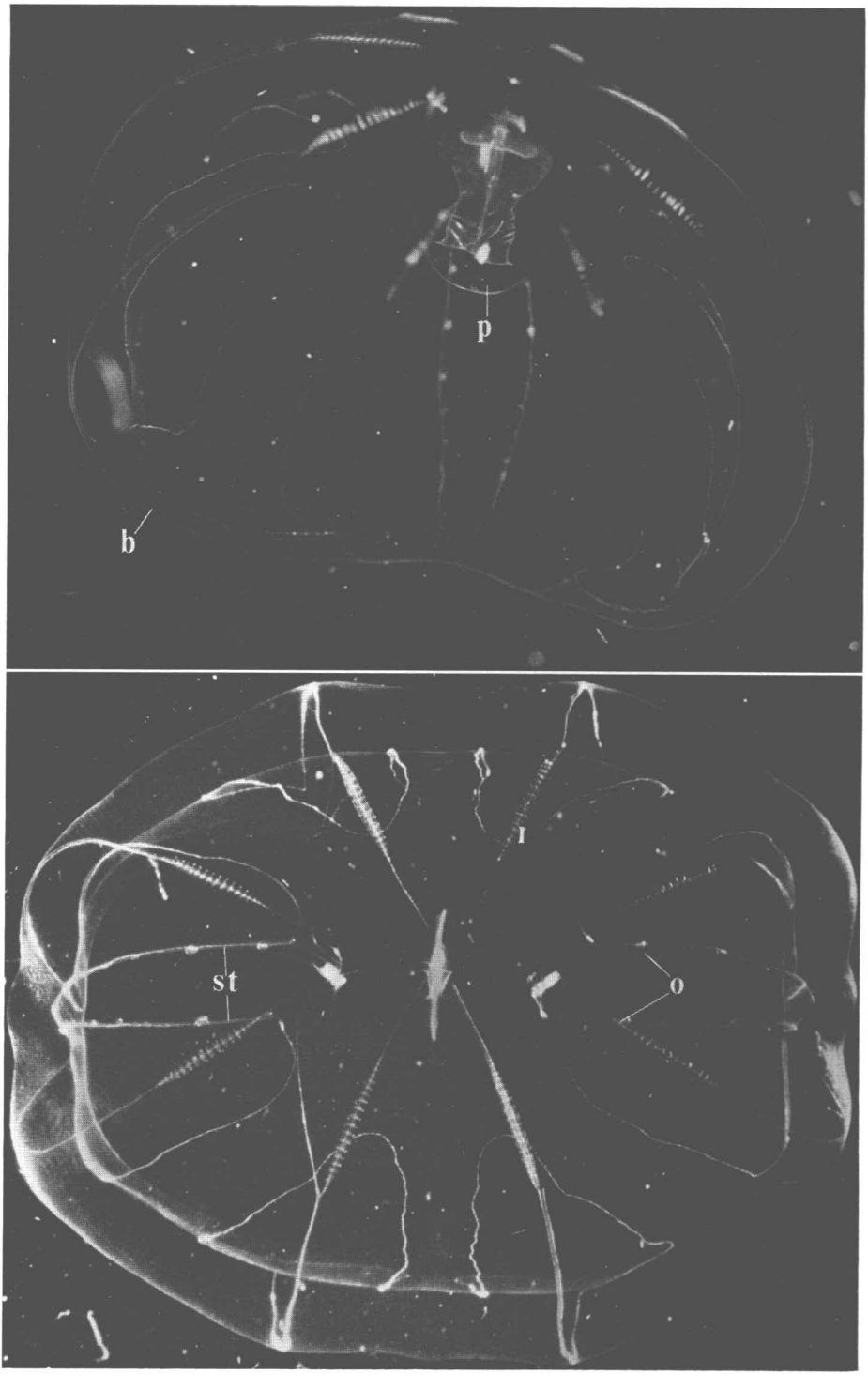
Diagnosis.—Tentaculate ctenophore with medusa-like body and central conical peduncle bearing gut and mouth. Lobes and auricles absent. Comb rows short. Tentacles with lateral filaments, but without tentacle sheaths.

Material examined.—Ten specimens, 30–50 mm in diameter. The largest individuals seen in the field were about 15 cm in diameter when fully open. The single, badly preserved specimen has been deposited in the U.S. National Museum of Natural History.

Description.—Resembles a medusa when fully expanded (Fig. 1), slightly oval in cross section, with longer axis in tentacular plane. In response to external stimuli, it contracts to a form resembling *Bolinopsis vitrea*, or to a two-globe form by pinching in around tentacular plane. Eight comb rows of equal length with 23 ctene plates each. Comb rows extend 0.25 to 0.33 of total oral–aboral distance.

Gut wide, flat, situated in central peduncle. Mouth slit-like, in stomodeal plane. Paragastric canals run down along flat sides of stomodeum, turn outward and end blindly at level of mouth. Gut somewhat constricted in center, with upper half expanded into digestive region. Funnel not well defined.

Arrangement of canals is shown in Figure 2. Broad funnel canal extends aborally from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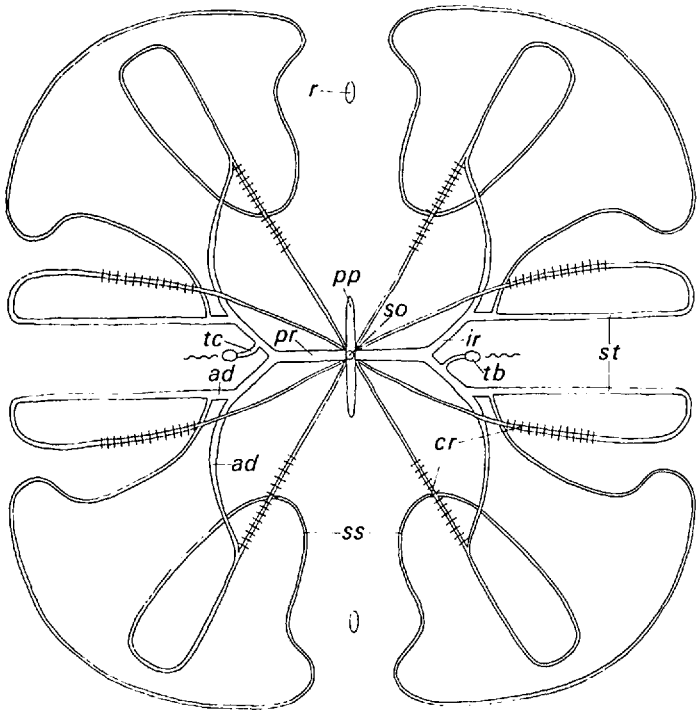

Figure 2. *T. inconstans*, semi-diagrammatic view from aboral pole, showing pattern of the canals. (ad—adradial canals; cr—comb row; ir—interradial canals; pp—pole plate; pr—perradial canals; r—ridges; so—statocyst; ss—subsagittal canals; st—subtentacular canals; tb—tentacle bulbs; tc—tentacle canals.)

top of gut to statocyst. Two perradial (= transverse) canals extend from sides of stomodeum, in tentacular plane, each branching into two interradial canals. Tentacle canals descend from each pair of interradials to tentacle bulbs. Interradials end by branching into two adradial canals, a short one connecting to subtentacular meridional canal and a longer one leading to subsagittal meridional canal. Subsagittal canals run beneath subsagittal comb rows on outer surface of bell-like body, return aborally on inner surface, loop back to edge of bell, follow its periphery for 0.25 of its circumference, finally return aborally, connecting to junction of adradial and subtentacular canals. Subtentacular canals run straight down to edge of bell, double back following subtentacular comb rows, and end blindly just past aboral ends of comb rows. Fine neurites connect aboral ends of all comb rows to statocyst. All canals are a golden color; subtentacular canals contain numerous large spherical ova in their descending limbs. Two short ridges arise midway along inside of bell, between descending subsagittal canals, but with no apparent connection to canals.

Tentacle bulbs situated on sides of central peduncle, halfway down the stomodeum.

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Figure 1. Live specimens of *Thalassocalyce inconstans*, photographed in aquaria. Upper. Lateral view showing stomodeal plane. Lower. Aboral view, longer axis is in the tentacular plane. Note ova in the subtentacular canals. (b—bell; p—peduncle; o—ova; st—subtentacular canals.)

Tentacles with simple lateral filaments hang freely into bell cavity, not enclosed in tentacle sheaths. Statocyst slightly sunken below aboral surface; pole plate extends about halfway to comb rows in stomodeal plane.

Live specimens have been maintained for as long as one week, with no indication of metamorphosis into any other form. We intend to follow with growth and development of *T. inconstans* at the earliest opportunity.

Discussion

We consider *Thalassocalyce inconstans* to be the adult form of a new genus and species of ctenophore and the basis of a new order, intermediate in morphology between the Cydippida and the Lobata. However, in view of the similarity between *T. inconstans* and three "medusoid" forms described by other authors (Chun, 1880; Moser, 1910; Dawydoff, 1948) one might argue that *T. inconstans* is an unusually large larval stage in the development of some species of lobate ctenophore. In considering this argument, we will compare the morphology of *T. inconstans* with that of other adult ctenophores and then with the three medusoid forms—a larva of *Leucothea multicornis* (Chun, 1880), a possible larval form called *Cryptolobata primitiva* (Moser, 1910) and a larva of *Ocyropsis* sp. (Dawydoff, 1948).

As described above, the principal distinguishing characters of *T. inconstans* are the absence of discrete lobes and auricles and the pattern of the meridional canals. Clearly, the medusoid bell is morphologically equivalent to two fused lobes. This homology is further indicated by the bilaterally symmetrical musculature of the bell which enables the ctenophore to pinch in around the tentacular plane. The course of the meridional canals appears unique among adult ctenophores. Figure 3a, b, and c are schematic representations of the arrangement of the gut, comb rows, and canals for species in three orders of ctenophores: Cydippida, Thalassocalycida, and Lobata.

T. inconstans shows clear resemblances to the cydippid pattern in the presence of perradial canals and blind paragastric canals. Further, the subtentacular and subsagittal canals are blind; none of the meridional canals connect with each other except where they branch from the adradial canals, as in cydippids. The loops in the subsagittal canals suggest those of lobates, however, and the overall pattern of the canals appears intermediate between the Cydippida and the Lobata.

Of the three "medusoid" ctenophores which are similar to *T. inconstans*, the presumed larva of *Leucothea multicornis* described by Chun (1880) is the best described and most closely resembles *T. inconstans*. This "medusiform larva" is illustrated in Figures 4a and b. These forms come between the cydippid larva and the *Bolinopsis*-stage larva in the ontogeny of *L. multicornis*. The body shape and canal pattern are similar to those of *T. inconstans*. Chun's largest specimen was 25 mm in diameter, considerably smaller than our specimens. Other important differences are: (1) The larva has only rudimentary tentacle bulbs and no tentacles; in *T. inconstans* bulbs and tentacles are simple, but fully developed. (2) The relative lengths and connections of the various canals differ. In the larva, the subtentacular canals are short, not reaching the edge of the bell, as in *T. inconstans*. The subsagittal canals of the larva merge with the subtentacular canals at the position of the presumptive auricle. Thus the subtentacular and subsagittal canals in each quadrant are joined, contrary to the case for *T. inconstans*. (3) The larva has rudimentary ctenes between the subtentacular canals, at the sites of the presumptive auricles. These are totally absent in *T. inconstans*. The small ridges on the inside of the bell in our specimens lie between the subsagittal canals, 90° from the position of the auricles in the larva. (4) All the specimens of *T. inconstans* which we have examined had ova developing in the descending limbs of the subtentacular canals. No sexual products were present in Chun's

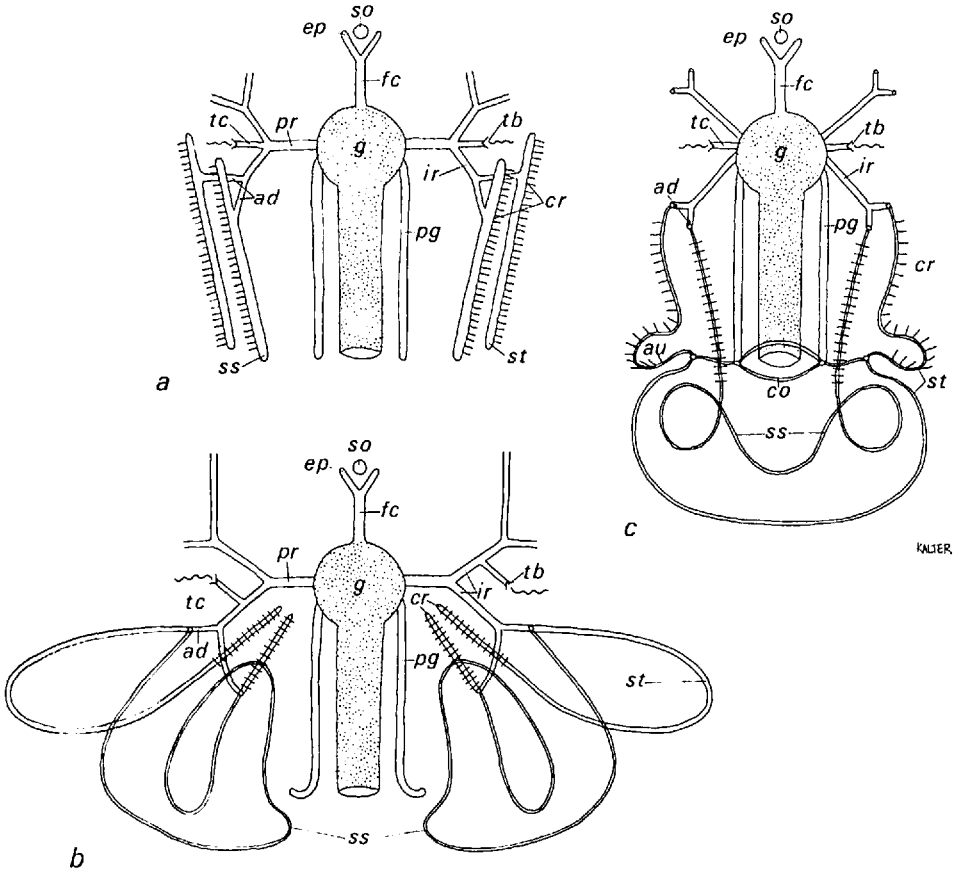

Figure 3. Diagrams of the canal patterns of three orders of ctenophores. a. Cydippida, modified from Krumbach, 1925. b. Thalassocalycida. c. Lobata, modified from Krumbach, 1925. (au—auricles; co—circum-oral canal; ep—excretory pore; fc—funnel canal; g—gut; pg—paragastric canals; other abbreviations as previous figures.)

larvae, although they did occur in the previous cydippid stage (Chun, 1880, 1892). (5) We have never collected *L. multicornis* and *T. inconstans* from the same area (Harbison, Madin, and Swanberg, 1978).

The enigmatic form *Cryptolobata primitiva* (Moser, 1910) was described from a single specimen, 1 mm in diameter after preservation in osmic acid. It is roughly spherical in shape, without lobes or auricles, and with a pointed aboral ridge in the tentacular plane. Because of its small size, Moser was unable to trace the connections in the vicinity of the funnel. The subtentacular canals run toward the oral edge and around its periphery, fusing with each other. The subsagittal canals on each side run orally and fuse with one another in a simple loop. Paragastric canals turn outward at the mouth and end blindly, as in Chun's larva and in *T. inconstans*. Between the subtentacular canals on each side there is a small depression, perhaps representing presumptive auricles. The tentacle bulbs are small and rudimentary, with no trace of tentacles. This form thus differs from *T.*

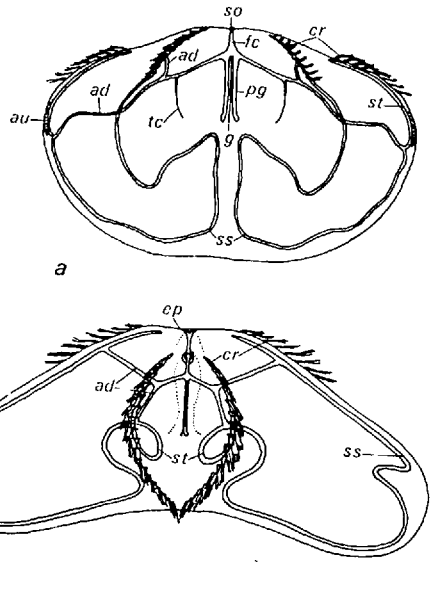

Figure 4. Medusoid larva of *Leucothea multicornis*. a. Side view of the stomodeal plane. b. Side view of the tentacular plane. Both from Chun, 1880. Abbreviations as previous figures.)

inconstans at least as much as does the *L. multicornis* larva, and we view the resemblances as superficial.

Dawydoff (1948) describes a stage in the development of *Ocyropsis* sp. which has a medusoid appearance, due to fusion of the presumptive lobes, forming a bell into which the stomach extends on a manubrium-like peduncle. No description of the canal pattern is given. This larval stage persists for only a short time before the lobes develop and the adult morphology appears. There seems little reason to suspect more than a passing resemblance to *T. inconstans*.

We see three possible ways in which *T. inconstans* may be allied to the forms we have discussed here, and to other ctenophores in general.

1) Although clearly not the same as the larvae of *L. multicornis* or *Ocyropsis* sp., *T. inconstans* may be a larval stage of some other species. Perhaps many lobates pass through a medusoid form, and we have found one that is unusually large.

2) *Thalassocalyce inconstans* may be an adult form, and either or both of the ctenophores described by Chun and Moser may be an earlier stage in its development. There is no evidence that Chun (1880) directly observed the metamorphosis of the cydippid larva into the medusoid, or the medusoid into the *Bolinopsis*-stage. After first thinking it to be a ". . . new aberrant lobate ctenophore . . . ," he placed it in the developmental cycle of *Leucothea* on the basis of ". . . various analogies which it offered to the previously mentioned [cydippid] stage, and the discovery of intermediate forms, which harmoniously connect the characters of the two larvae . . ." (Chun, 1880, p. 127).

3) *T. inconstans* may be an adult form, and the larval stages described by Chun and Dawydoff may represent recapitulations of the thalassocalycid morphology during the development of *Leucothea* and *Ocyropsis*. Such phylogenetic reminiscence is a well-known feature of ctenophore ontogeny. *Bolinopsis vitrea* passes through a cydippid stage (Agassiz, 1865); *Mnemiopsis leidyi* through cydippid and *Bolinopsis*-stages (Mayer, 1912), *Ocyropsis* and *Leucothea* through cydippid, medusoid and *Bolinopsis*-stages. As suggested earlier, the morphology of *T. inconstans* is intermediate between that of the Cydippida and the Lobata, perhaps corresponding in phylogeny to the position of the medusoid larva in ontogeny.

We favor the last possibility. Several features of our specimens: the large size, the mature ova, the functional tentacles, the absence of apparent "Anlagen" for lobate morphology or any indication of metamorphosis, all argue that *T. inconstans* is an adult form. If so, its unique morphology entitles it to distinction at the ordinal level, and an important place in ctenophore phylogeny.

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